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EVOLUTIONARY ECOLOGY OF MOUNTAIN BIRCH IN SUBARCTIC STRESS GRADIENTS: INTERPLAY OF BIOTIC AND ABIOTIC FACTORS IN PLANT-PLANT INTERACTIONS AND EVOLUTIONARY PROCESSES

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ABSTRACT

In nature, variation for example in herbivory, wind exposure, moisture and pollution impact often creates variation in physiological stress and plant productivity. This variation is seldom clear-cut, but rather results in clines of decreasing growth and productivity towards the high-stress end. These clines of unidirectionally changing stress are generally known as 'stress gradients'. Through its effect on plant performance, stress has the capacity to fundamentally alter the ecological relationships between individuals, and through variation in survival and reproduction it also causes evolutionary change, i.e. local adaptations to stress and eventually speciation. In certain conditions local adaptations to environmental stress have been documented in a matter of just a few generations.

In plant-plant interactions, intensities of both negative interactions (competition) and positive ones (facilitation) are expected to vary along stress gradients. The stress-gradient hypothesis (SGH) suggests that net facilitation will be strongest in conditions of high biotic and abiotic stress, while a more recent 'humpback' model predicts strongest net facilitation at intermediate levels of stress. Plant interactions on stress gradients, however, are affected by a multitude of confounding factors, making studies of facilitation-related theories challenging. Among these factors are plant ontogeny, spatial scale, and local adaptation to stress. The last of these has very rarely been included in facilitation studies, despite the potential co-occurrence of local adaptations and changes in net facilitation in stress gradients. Current theory would predict both competitive effects and facilitative responses to be weakest in populations locally adapted to withstand high abiotic stress.

This thesis is based on six experiments, conducted both in greenhouses and in the field in Russia, Norway and Finland, with mountain birch (*Betula pubescens* subsp. *czerepanovii*) as the model species. The aims were to study potential local adaptations in multiple stress gradients (both natural and anthropogenic), changes in plant-plant interactions under conditions of varying stress (as predicted by SGH), potential mechanisms behind intraspecific facilitation, and factors confounding plant-plant facilitation, such as spatiotemporal, ontogenetic, and genetic differences.

I found rapid evolutionary adaptations (occurring within a time-span of 60 to 70 years) towards heavy-metal resistance around two copper-nickel smelters, a phenomenon that has resulted in a trade-off of decreased performance in pristine conditions. Heavy-metal-adapted individuals had lowered nickel uptake, indicating a possible mechanism behind the detected resistance. Seedlings adapted to heavy-metal toxicity were not co-resistant to others forms of abiotic stress, but showed co-resistance to biotic stress by being consumed to a lesser extent by insect herbivores. Conversely, populations from conditions of high natural stress (wind, drought etc.) showed no local adaptations, despite much longer evolutionary time scales.

Due to decreasing emissions, I was unable to test SGH in the pollution gradients. In natural stress gradients, however, plant performance was in accordance with SGH, with the strongest host-seedling facilitation found at the high-stress sites in two different stress gradients. Factors confounding this pattern included (1) plant size / ontogenetic status, with seedling-seedling interactions being competition dominated and host-seedling interactions potentially switching towards competition with seedling growth, and (2) spatial distance, with competition dominating at very short planting distances, and facilitation being strongest at a distance of circa ¼ benefactor height. I found no evidence for changes in facilitation with respect to the evolutionary histories of plant populations. Despite the support for SGH, it may be that the 'humpback' model is more relevant when the main stressor is resource-related, while what I studied were the effects of 'non-resource' stressors (i.e. heavy-metal pollution and wind).

The results have potential practical applications: the utilisation of locally adapted seedlings and plant facilitation may increase the success of future restoration efforts in industrial barrens as well as in other wind-exposed sites. The findings also have implications with regard to the effects of global change in subarctic environments: the documented potential by mountain birch for rapid evolutionary change, together with the general lack of evolutionary 'dead ends', due to not (over) specialising to current natural conditions, increase the chances of this crucial forest-forming tree persisting even under the anticipated climate change.

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following publications, referred to in the text by their Roman numerals

I ERÄNEN J.K. (2008) Rapid evolution towards heavy metal resistance by mountain birch around two subarctic copper-nickel smelters
Journal of Evolutionary Biology 21, 492-501

II ERÄNEN J.K., NILSEN J., ZVEREV V.E. & KOZLOV M.V. Mountain birch under multiple stressors – heavy metal resistant populations co-resistant to biotic stress but mal-adapted to abiotic stress
Journal of Evolutionary Biology, in press

III ERÄNEN J.K. & KOZLOV M.V. (2006) Physical sheltering and liming improve survival and performance of mountain birch seedlings: a 5-year study in a heavily polluted industrial barren
Restoration Ecology 14, 77-86

IV ERÄNEN J.K. & KOZLOV M.V. (2007) Competition and facilitation in industrial barrens: variation in performance of mountain birch seedlings with distance from nurse plants
Chemosphere 67, 1088-1095

V ERÄNEN J.K. & KOZLOV M.V. (2008) Increasing intraspecific facilitation in exposed environments: consistent results from mountain birch populations in two subarctic stress gradients
Oikos 117, 1569-1577

VI ERÄNEN J.K. & KOZLOV M.V. (2009) Interactions between mountain birch seedlings from differentiated populations in contrasting environments of subarctic Russia
Plant Ecology 200, 167-177

1. INTRODUCTION

1.1. A very brief history of the role of biotic and abiotic forces in biological theory

Ever since Charles Darwin coined his famous evolutionary theory in *The Origin of Species*, and even earlier (Darwin 1859; Singer 1951), interactions between individual organisms have been considered to be of fundamental importance in nature, and through their effect on fecundity and survival also a causal reason behind adaptive evolution. Within-species differentiation and adaptation has been studied for at least 200 years in economically important species (sensu Linhart & Grant 1996), and for over a century also in natural populations (e.g. Schmidt 1899; Turesson 1922, 1925; Clausen *et al.* 1940). Already in the early days there was controversy over the relative importance of biotic factors, i.e. competition, and of the abiotic environment as drivers of evolutionary change. While Darwin himself believed firmly in the overwhelming importance of competition, stating for example in the 6th edition of *The Origi*n that "*we have reason to believe that only few plants or animals range so far, that they are destroyed exclusively by the rigours of the climate*" (Darwin 1872), some early naturalists emphasised the role of the environment, i.e. of abiotic factors, in creating selection pressure and driving adaptive evolution (sensu Darwin 1859; Bijlsma & Loeschcke 2005). Although nowadays both biotic and abiotic effects are recognised as fundamental factors in ecology and evolution, their relative importance is still a hot topic, as seen for example in the long-lasting debate concerning the effect of competition under conditions of varying abiotic stress (Grime 1973, 1979; Tilman 1982, 1988; Grace 1991; Holmgren *et al.* 1997; Goldberg *et al.* 1999; Craine 2005). More recently, academic controversy has arisen over the interplay between negative biotic interactions (competition) and positive ones (facilitation) in relation to abiotic stress (Bertness & Callaway 1994; Callaway 1995, 2007; Callaway & Walker 1997; Callaway *et al.* 2002; Maestre & Cortina 2004; Maestre *et al.* 2005, 2006; Lortie & Callaway 2006; Michalet *et al.* 2006; Brooker *et al.* 2008), and over the role player by adaptive evolution (namely stress resistance / tolerance) in these processes (Choler *et al.* 2001; Liancourt *et al.* 2005; Espeland & Rice 2007; Wang *et al.* 2008).

1.2. Evolutionary effects of spatial and temporal variation in environmental conditions

1.2.1. Local adaptation to stress and the surrounding environment in general

Individuals with the best traits in relation to performance in any given environment are likely to be the most successful at procreating; given their heritability, these traits

will become increasingly common in local populations with each passing generation. In studies conducted within species at contemporary timescales, this process of adaptive evolution, eventually leading to speciation, is usually called 'local adaptation' (or 'ecotypic differentiation') (see reviews by e.g. Futuyma & Moreno 1988; Linhart & Grant 1996; Briggs & Walters 1997; Orr & Smith 1998; Kawecki & Ebert 2004; Bijlsma & Loeschcke 2005; Savolainen *et al.* 2007). Evolutionary adaptations can arise in response to practically any abiotic or biotic factor that affects the survival or reproduction of individuals, with adaptations evolved with respect to for example food quality (Carroll *et al.* 1998; Codron *et al.* 2007), heavy-metal toxicity (Gregory & Bradshaw 1965; Watmough & Dickinson 1995; Dechamps *et al.* 2008), predation (Declerck & Weber 2003; Sandoval & Crespi 2008), drought (Knight *et al.* 2006; Franks *et al.* 2007), drag forces imposed by wind and water flow (Speck 2003; Harder *et al.* 2004), and herbivory (Sork *et al.* 1993; Núñez-Farfan *et al.* 2007). Local adaptations can stem either from the occurrence of novel mutations, or from selection on pre-existing (i.e. 'standing') genetic variation (Barrett & Schluter 2008). High levels of specialisation, i.e. local adaptation, often carry a cost of reduced performance under non-local conditions, effectively preventing the local genetic adaptations from becoming 'global' (Futuyma & Moreno 1988; Briggs & Walters 1997; Orr & Smith 1998; Kawecki & Ebert 2004; Bijlsma & Loeschcke 2005; Roff & Fairbairn 2007). Such trade-offs, and the resulting dominance of different genotypes at different points in time and space, can result in divergent evolution, forming part of the very foundation of contemporary evolutionary ecology. In some cases, however, genetic adaptation to one stressor can result in increased resistance to others, a phenomenon documented at least between different heavy metals (Watmough & Dickinson 1995; Utriainen *et al.* 1997) and between heavy metals and biotic stressors (reviewed by Poschenrieder *et al.* 2006). This phenomenon, known as 'co-resistance' or 'co-tolerance', acts quite oppositely to traditional trade-offs, but has mostly been studied only in the context of heavy-metal pollution (Watmough & Dickinson 1995; Utriainen *et al.* 1997; Sgherri *et al.* 2001; Zalecka & Wierzbicka 2002). Adaptations to heavy metals were also among the first examples of rapid evolutionary adaptation in nature (see e.g. Gregory & Bradshaw 1965; Simon 1978; Bradshaw & McNeilly 1981). Indeed, it is nowadays understood that given sufficient selection pressure, local genetic adaptation can occur in a matter of just a few generations (Huey *et al.* 2000; Franks *et al.* 2007; Van Doorslaer *et al.* 2007). Due to its contemporary nature, this process also has practical implications for conservation biology and restoration ecology (Stockwell *et al.* 2003; Hufford & Mazer 2003; Kinnison *et al.* 2007).

1.2.2. Factors affecting, and alternatives to, local adaptation

Factors favouring the formation of local adaptations include strong directional selection, low levels of gene flow (i.e. high levels of reproductive isolation) and stability of the selective environment (Futuyma & Moreno 1988; Linhart & Grant 1996; Briggs & Walters

1997; Orr & Smith 1998; Nunney 2001; Kawecki & Ebert 2004; Bijlsma & Loeschcke 2005; Savolainen *et al.* 2007). Under conditions of strong gene flow (via pollen, seeds, individuals etc.) or a variable environment, generalisation and phenotypic plasticity (see below) may prove safer and more successful strategies than local adaptation. In such cases the offspring may end up living in an environment vastly different to that experienced by their ancestors, in which case any adaptations to paternal or maternal conditions will be harmful (assuming that these adaptations carry a cost; see above). Generalists are "jacks of all trades, but masters of none"; theoretically they outperform locally adapted specialists across the selective environment, but are outperformed by specialists in their local environment, providing more 'margin for error' in unpredictable environments (Wilson & Yoshimura 1994; Futuyma 2001; Abrams 2006). Whereas true generalists are expected to use the same strategy and phenotype irrespective of the environment, phenotypically plastic individuals are capable of producing different phenotypes depending on the surrounding environment (Via *et al.* 1995; Schlichting & Pigliucci 1998; Pigliucci 2001; Kingsolver *et al.* 2002; Nussey *et al.* 2007). While phenotypic plasticity is often considered as a generalist strategy and an alternative to local adaptation, selection can act also on plasticity itself. In spatiotemporally heterogeneous environments, where different phenotypes are clearly superior under their respective conditions, adaptive phenotypic plasticity may be the most viable strategy (Via *et al.* 1995; van Kleunen & Fischer 2005; Holeski 2007; Lind & Johansson 2007). While adaptive phenotypic plasticity may sound like the ultimate evolutionary strategy, with optimal phenotypes produced in any given environment, the costs and limits associated with phenotypic plasticity (DeWitt *et al.* 1998; van Kleunen & Fischer 2005) make local adaptation a more successful evolutionary strategy under spatially and temporally stable conditions.

1.3. Competition, facilitation, and the stress-gradient hypothesis

Despite some early work suggesting positive interactions (facilitation) between plants (Phillips 1909; Magistad & Breazeale 1929; Ovington 1955), the results did not arouse much scientific interest, probably due to the then prevailing general consensus as to the overwhelming importance of negative plant-plant interactions (competition). Plant facilitation and its theoretical implications gained attention in the late 1980s (DeAngelis *et al.* 1986; Hunter & Aarssen 1988; Bertness 1988), spurring a renewed interest on the subject (e.g. Carlsson & Callaghan 1991; Callaway *et al.* 1991; Bertness & Shumway 1993; Aguiar & Sala 1994). A theoretical framework for the occurrence and importance of facilitation was first phrased by Bertness and Callaway (1994), whose 'stress-gradient hypothesis' (SGH) suggests that the relative importance of facilitation would increase with increasing biotic and abiotic stress (Bertness & Callaway 1994; Callaway 1995, 2007; Holmgren *et al.* 1997; Brooker & Callaghan 1998; Callaway *et al.* 2002; Bruno *et al.* 2003; Brooker *et al.* 2008). Although SGH also implies biotic stress, e.g. herbivory,

a huge majority of experiments have been conducted on gradients of abiotic stress (see Callaway 2007 and references therein).

The relative increase in facilitation with increasing stress, as predicted by SGH, is suggested to stem from two co-occurring phenomena. First, under deteriorating conditions decreasing plant growth will also lessen the importance of competition, as suggested already in the 1970s (Grime 1973, 1979; Grace 1991; Corcket *et al.* 2003; Craine 2005). Logically, this should hold true especially in cases when the primary factor limiting plant growth is switched from a critical (and strongly competed) plant resource under low-stress conditions to a non-resource stressor (e.g. wind, salinity etc.) under high-stress conditions. The situation may be more complex when the stressor too is resource-related (see 1.3.2. and Maestre & Cortina 2004; Maestre *et al.* 2005; Callaway 2007; Brooker *et al.* 2008). Second, with increasing negative effects of stress, the amelioration of growth conditions by nurse trees and/or grouping will become more important (Bertness & Callaway 1994; Callaway 1995, 2007; Holmgren *et al.* 1997; Callaway & Walker 1997; Brooker & Callaghan 1998; Brooker *et al.* 2008). The combined effect of these two phenomena should result in increasing net facilitation, as predicted by SGH. Increasing facilitation can result from a multitude of mechanisms, including direct mitigation of various abiotic stressors (Carlsson & Callaghan 1991; Shevtsova *et al.* 1995; Callaway *et al.* 1996; Holmgren *et al.* 1997; Caldwell *et al.* 1998; Wied & Galen 1998; Gerdol *et al.* 2000; Pugnaire & Luque 2001; Brooks *et al.* 2002; Rigg *et* al. 2002; Smith *et al.* 2003; Armas & Pugnaire 2005; Eckstein & Donath 2005; Baumeister & Callaway 2006; Reisman-Berman 2007; Zvereva & Kozlov 2007), and indirect mitigation of field layer competition and herbivory (Levine 1999; Pages *et al.* 2003; Stiling *et al.* 2003; Oesterheld & Oyarzabal 2004; Bossuyt *et al.* 2005; Kunstler *et al.* 2006). Indeed, support for SGH has been detected in a wealth of studies and with respect to a multitude of stressors (for a comprehensive review see Callaway 2007).

1.3.1. Factors potentially confounding the predictions of SGH

In nature, of course, nothing is as simple as suggested in the previous section. The performance, survival and reproduction of individual plants is affected by multiple abiotic and biotic factors, creating variation in plant interactions and potentially confounding the results of studies on SGH.

1.3.1.1. Spatial variation

Both competition and facilitation are generally considered to be omnipresent in plant communities, but their intensities vary independently of each other with distance between plants. Positive effects of trees on microclimate have been detected at distances exceeding tree height by up to 8 – 50 times (Den Uyl 1936; Stoeckler & Dortignac 1941; Heisler & Dewalle 1988), while the most intense competition is usually limited to distances under 0.5 – 1 times tree height (Kort 1988; Kowalchuk & De Jong 1995; Sudmeyer *et al.* 2002). As a result, plant performance is expected to peak at intermediate

distances, with inhibitory effects hampering plant performance at short distances and weakening facilitation lessening it further away. Very few studies have addressed this issue; most experiments have merely contrasted 'sheltered' and 'exposed' situations, thus overlooking all information on the spatial scales at which plant-plant interactions operate. In a rare study, Dickie and his colleagues (2005) studied the spatially disjunct effects of plant facilitation and competition, and indeed found net facilitation to be strongest at intermediate distances. Inappropriate choice of distance between study plants can thus result in underestimating facilitation and overestimating competition, masking potentially important facilitative interactions.

1.3.1.2. Temporal variation

Fluctuating environmental conditions can create variation in plant-plant interactions, with facilitation dominating during harsh periods and competition increasing in importance in more lenient phases (Berkowitz *et al.* 1995; Greenlee & Callaway 1996; Casper 1996; Gómez-Aparicio *et al.* 2004; Kikvidze *et al.* 2006) or vice versa (Armas & Pugnaire 2005). Temporal variation in plant interactions can also result from the size and ontogenetic stage of the beneficiary, with facilitation dominating in the seedling phase and competition becoming more important with plant growth and development (Callaway & Walker 1997; Rousset & Lepart 2000; Kunstler *et al.* 2006; Miriti 2006; Sthultz *et al.* 2007). Plant-plant interactions may be affected by the size not only of the beneficiary but also of the benefactor, with larger plants having a stronger effect – whether positive (Pugnaire *et al.* 1996; Tewksbury & Lloyd 2001) or negative (Klanderud & Totland 2004; Reisman-Berman 2007) – on the surrounding vegetation. In studies on even-aged assemblages, the switches in interactions can be even more intricate (Goldberg *et al.* 2001). When interactions are studied in plants of a particular size and developmental status, or in years that are more lenient than usual, facilitative interactions may thus go undetected despite their putative importance at a different point in time.

1.3.1.3. Variation driven by stress resistance

Different species can inflict and respond to facilitation differently (Callaway 1998, 2007; Blignaut & Milton 2005; Klanderud & Totland 2005; Pages & Michalet 2006). Taxonomically closely related species are more likely to compete with than facilitate each other (Valiente-Banuet & Verdú 2008), and stress-resistant species benefit less from facilitation than susceptible ones (Choler *et al.* 2001; Liancourt *et al.* 2005; Wang *et al.* 2008). Together with the often observed negative association between stress resistance and competitive ability (Linhart & Grant 1996; Briggs & Walters 1997; Orr & Smith 1998; Corcket *et al.* 2003; Kawecki & Ebert 2004; Bijlsma & Loeschcke 2005), stress-resistant species are less likely to be positively affected by facilitation, and more likely to suffer from competition. Thus failure to detect facilitation in a model species should not be (over)generalised across the community.

Thinking more holistically, within-species differences in stress resistance, i.e. local adaptation to stress, can also have strong implications for plant interactions in stress gradients, and may have contributed to inconsistencies in the results of earlier experiments. More will be said about the combined effect of local adaptation and plant interactions in stress gradients in section 1.4.

1.3.2. Challenging SGH – the 'humpback' model

Studies that do not include the entire stress gradient (i.e. almost all ecological experiments) risk over-emphasising either competition or facilitation by focusing on the low- or high-stress ends of the study gradients respectively (Maestre & Cortina 2004; Maestre *et al.* 2005; Lortie & Callaway 2006; Kawai & Tokeshi 2007; Callaway 2007). The "location" of study sites along the stress gradient is especially crucial if the combined effect of competition and facilitation does not change linearly with stress. This suggestion, conflicting with one of the core assumption of SGH, has arisen from studies on nutrient and aridity gradients, with increasing competition for the resource stressor suggested to switch the balance from facilitation back to competition at the very extreme end of the stress gradient; this results in a 'humped-back' curve, with facilitation dominating only at intermediate levels of stress (Rebele 2000; Maestre & Cortina 2004; Maestre *et al.* 2005; Gilad *et al.* 2007). Such a switch in net interactions, together with study conditions overemphasising the high-stress end of the stress gradient, may explain why some experiments have found increasing net competition with increasing stress (Blignaut & Milton 2005; Armas & Pugnaire 2005), a response opposite to that predicted by SGH. The conflicting predictions of the two models have created some heated debate on the generality of SGH (Maestre *et al.* 2005, 2006; Lortie & Callaway 2006; Callaway 2007). One important point, which to my knowledge has been largely ignored in the ongoing discussion, is the nature of the main stressor. Studies suggesting the dominance of competition at both ends of the stress gradient (the humpback model) assume a 'resource stressor' (drought or lack of nutrients) to be the most important abiotic force affecting plant-plant interactions (Rebele 2000; Maestre & Cortina 2004; Maestre *et al.* 2005; Gilad *et al.* 2007). While it is likely that extreme shortage of a primary resource (e.g. water or nutrients) will result in strong competition, possibly shifting the balance away from facilitation at the extreme end of the stress gradient, increasing competition for a 'non-resource stressor' (e.g. wind) is a theoretical impossibility. While facilitation itself may decline in exceptionally severe environments (sensu Michalet *et al.* 2006), the effect of decreasing facilitation (assumed for non-resource stressors) is likely to be negligible compared to its joint effect with increasing competition (assumed for resource stressors) in conditions of extreme stress. I therefore suggest that the nature of the main stressor may be important with regard to the effect of stress on plant-plant interactions, with the effects of non-resource stressors agreeing better with the predictions of SGH.

Altogether, given the large number of confounding effects which have received little to no attention, it is no surprise that a number of studies, especially in arid environments, have failed to find support for SGH (Casper 1996; Donovan & Richards 2000; Maestre *et al.* 2005; Armas & Pugnaire 2005; Dullinger *et al.* 2007; Malkinson & Jeltsch 2007). More experiments, in a multitude of environmental gradients, are clearly needed to determine the generality of SGH and the importance of the confounding factors, in order to provide a better understanding of the patterns and mechanisms behind changes in plant-plant interactions.

1.4. Synthesising the two phenomena: the understudied interplay of local adaptation and facilitation in stress gradients

The recently renewed interest in positive plant interactions also has implications on a community scale (Bruno *et al.* 2003; Lortie *et al.* 2004; Michalet *et al.* 2006; Callaway 2007). Including facilitation in the classic model by Grime (1973) helps us better understand productivity-diversity relationships, with increasing facilitation at intermediate to high levels of stress creating favourable conditions for species susceptible to stress and thereby increasing biodiversity (Michalet *et al.* 2006). Despite the strong implications of stress resistance for plant interactions in stress gradients, and potentially co-occurring local adaptations to stress, the effects of stress resistance on facilitative responses have generally been studied only in an among-species context (Choler *et al.* 2001; Liancourt *et al.* 2005; Wang *et al.* 2008). This is especially surprising considering the large number of studies on local adaptation (1.2.1) and facilitation (1.3) in stress gradients, as well as the established role of facilitation in evolutionary processes (Odling-Smee *et al.* 1996; Laland *et al.* 1999; Valiente-Banuet *et al.* 2006; Lortie 2007) and conversely the role played by evolutionary adaptations in facilitation (Choler *et al.* 2001; Liancourt *et al.* 2005; Wang *et al.* 2008).

Despite the importance of biotic factors, abiotic stressors and the related adaptations for plant interactions and community organisation, to my knowledge only one article, written in the course of my work on this thesis, has been published on the interplay between local adaptation and plant facilitation. In their pioneering work, Espeland and Rice (2007) suggest that as the effects of stress adaptation on the competitive ability of individual plants are well established (Futuyma & Moreno 1988; Briggs & Walters 1997; Orr & Smith 1998; Kawecki & Ebert 2004; Bijlsma & Loeschcke 2005; Roff & Fairbairn 2007), it would seem reasonable that facilitative responses would similarly vary within species among differently adapted populations. They argue, as previously suggested in an among-species context, that individuals adapted to local conditions are less reliant on facilitation, and that facilitation is most important for plants growing away from their environmental optima (Espeland & Rice 2007). Indeed, they found that facilitation was especially important for non-serpentine individuals growing in stressful

serpentine soil, supporting the original argument. If backed by other experimental studies, the detected pattern would increase the likelihood of competitive exclusion of stress-adapted individuals, already known to often exhibit decreased competitive ability (Futuyma & Moreno 1988; Briggs & Walters 1997; Orr & Smith 1998; Kawecki & Ebert 2004; Bijlsma & Loeschcke 2005; Roff & Fairbairn 2007). The effect of local adaptation on facilitation would create yet another variable to take into account in models of community organisation (Bruno *et al.* 2003; Lortie *et al.* 2004; Michalet *et al.* 2006; Callaway 2007), with within-species differences in stress resistance creating similar variation as among-species differences. Finally, the discrepancy in responses to facilitation may create yet another confounding factor (see 1.3.1), with the choice of the study population potentially preventing the researcher from detecting increasing facilitation, despite its putative importance at the species level.

The inclusion of stress resistance in models of plant interactions in stress gradients may sound very academic, but it is not a purely theoretical issue. Local adaptations to stress are most likely to occur in harsh environments, such as alpine, arctic and arid systems, where facilitation is likewise expected to be most apparent. The same systems are also the most sensitive to anthropogenic change, including global change and invasive species. In order to successfully manage and conserve these systems, knowledge is needed of the role of biotic and abiotic factors, and their interactions, on plant and animal communities. Thus plant interactions, including facilitation, the pace of evolutionary change, and their interacting effects are of major importance in applied sciences as well, including restoration ecology and conservation biology (Stockwell *et al.* 2003; Hufford & Mazer 2003; Gómez-Aparicio *et al.* 2004; Padilla & Pugnaire 2006; Kinnison *et al.* 2007).

1.5. Objectives of the study

The general objectives of this thesis were to understand the ecological and evolutionary effects of abiotic stress and biotic interactions in multiple stress gradients in subarctic environments, with mountain birch (*Betula pubescens* subsp. *czerepanovii* (Orlova) Hämet-Ahti) as the model species. The general assumptions at the beginning of working with this thesis were that the positive net effect of plants on surrounding vegetation would increase with abiotic stress, and that abiotic stress has the potential, through creating different selective regimes, to drive divergent evolution and thus local adaptations. Advances in ecological theory forced an amendment to the first assumption, with consideration given to the possibility that the net effect of facilitation is at its strongest in intermediate levels of stress. More specific questions I aimed to answer were:

1. Has high abiotic stress resulted in local adaptation of mountain birch populations in some of the stress gradients studied?
2. Do the putative adaptations result in trade-offs of reduced performance in non-local conditions, or conversely co-resistance to other stressors?

3. What are the spatial scales at which co-occurring competition and facilitation operate, and what are the potential mechanisms behind plant-plant facilitation?
4. Does the role of intraspecific facilitation increase with increasing abiotic stress, and can the results be generalised across multiple stress gradients?
5. Are the effects of co-occurring competition and facilitation dependent on the size and ontogenetic stage of the interacting plants?
6. Are the competitive responses and facilitative effects of mountain birch seedlings dependent on the evolutionary histories of local populations?

To answer these questions I conducted a set of experiments in Russia, Norway and Finland with mountain birch seedlings originating from the Kola Peninsula, northwestern Russia. Experiments **I** and **II** were conducted to study local adaptations to anthropogenic and natural stressors, and potential trade-offs and co-resistances. Experiments **III** and **IV** were aimed at studying the mechanisms and spatial scales at which competition and facilitation operate in high-stress environments. The role of facilitation in gradients of abiotic stress was studied in experiments **V** and **VI**. Both experiments incorporated plant interactions and stress gradients, with experiment **V** also taking into account the ontogenetic stage of the benefactors. In experiment **VI** I attempted to synthesise local adaptation and SGH by taking into account the evolutionary history of the plant populations, i.e. potential local adaptations to stress.

2. MATERIALS AND METHODS

2.1. Study species

All the studies were conducted with mountain birch, which has been the dominant tree species in northern Fennoscandia and northwestern Russia since the last ice age some 10 000 year ago (Aas & Faarlund 2001). Although the taxonomic status of mountain birch is debatable (Jonsell 2000; Mäkinen 2002), I prefer to use the subspecific name *B. pubescens* subsp. *czerepanovii*, which allows for an accurate identification of the study object regardless of possible future changes in taxonomy. In the northern boreal zone, mountain birch often forms mixed forests together with Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.), as well as – especially at higher altitudes and latitudes – monospecific forests up to the timberline (Wielgolaski 2001). In favourable growth conditions, for instance when nutrients are plentiful (Wielgolaski & Nilsen 2001), pollution loads are low (Kryuchkov 1993) and wind shelter is available (Wielgolaski & Nilsen 2001; Aradottir *et al.* 2001), mountain birches generally grow as single trunk (monocormic) trees. Under stressful conditions, such as heavy pollution (Kryuchkov 1993; Kozlov & Zvereva 2007), strong winds (Wielgolaski & Nilsen 2001; Aradottir *et al.* 2001), nutrient poor soil (Wielgolaski & Nilsen 2001) or heavy herbivory (Wielgolaski 2001), mountain birches grow as multi-stem (polycormic) bushes, with a height of only 1 to 2 m (Figure 2). The low growth form may be a phenotypic response to stress (Kozlowski *et al.* 1991; Kozlowski & Pallardy 2002), or a genetic adaptation to an extreme environment (**II**). In general, since it forms viable populations up to the timberline (Wielgolaski 2001) and survives in the heavily polluted industrial barrens of the Kola Peninsula (Kryuchkov 1993; Kozlov & Zvereva 2007), mountain birch is considered a stress-resistant species. Although stress-resistant species may not be optimal candidates for facilitation studies (Choler *et al.* 2001; Liancourt *et al.* 2005; Wang *et al.* 2008), due to the harsh conditions of my high-stress study sites (see below) a species that could withstand high abiotic stress was needed.

2.2. Source sites

All the seedlings used in the experiments originated from various populations in the Kola Peninsula, northwest Russia (between 66 – 70 degrees north and 29 – 41 degrees east; Figure 1). The Kola Peninsula, bordered by the White Sea to the south and the Arctic Ocean to the north, is characterised by boreal forests in its southern parts and subarctic tundra in the north. Mountain ranges up to 1200 m a.s.l. can be found in the central parts, and the entire peninsula is characterised by a dense hydrological net, with numerous lakes, swamps and rivers. The climate is maritime along the coasts and moderately continental inland. Mean

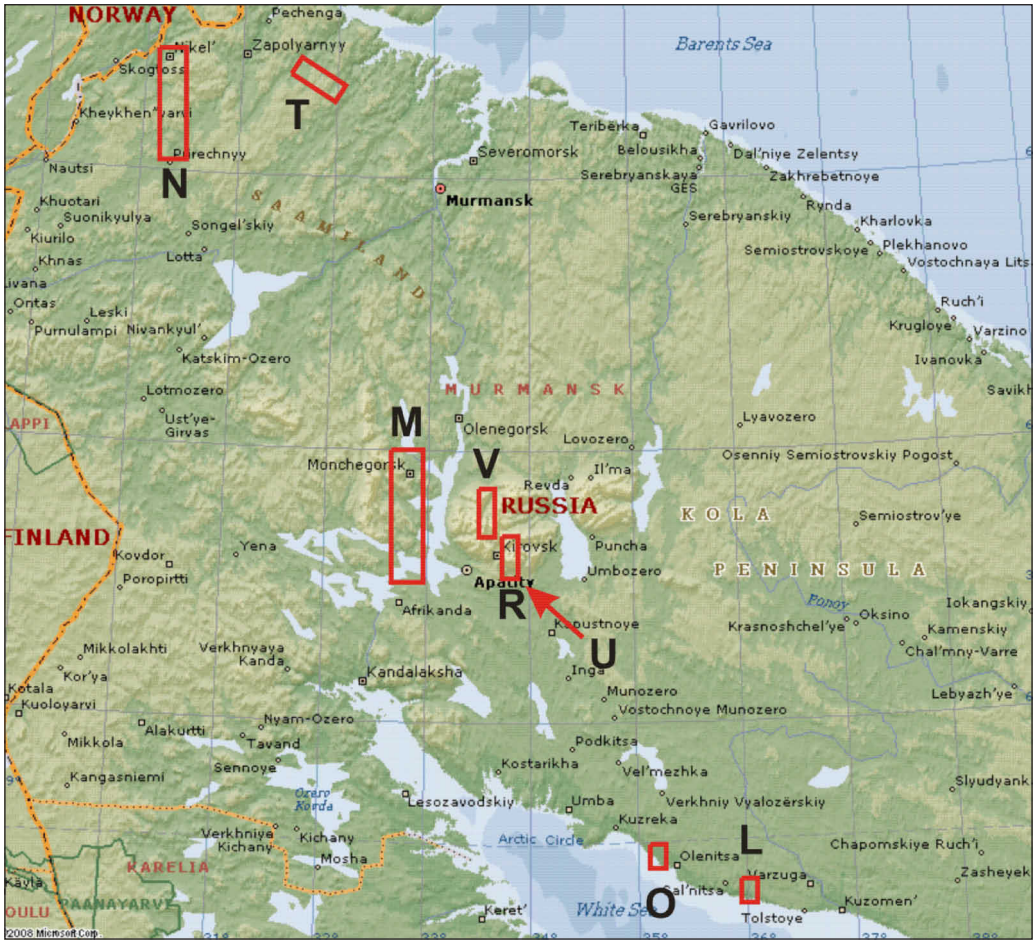

Figure 1. Locations of source populations used in the thesis: L = seashore gradient near the mouth of the river Lodochnyi (used in article **I**); M = pollution gradient around the Severonikel smelter in Monchegorsk (**I**; **II**; **VI**); N = pollution gradient around the Pechenganikel smelter in Nikel (**I**; **II**); O = seashore gradient near the mouth of the river Olenitsa (**I**; **II**; **V**; **VI**); R = elevation gradient on mount Raswumchorr / Lovchorr (**I**; **II**; **V**; **VI**); T = open tundra sites (**II**); U = unpolluted and sheltered site (**III**; **IV**); V = elevation gradient on mount Vudjavr / Kukisvumchorr (**I**; **II**).

annual precipitation ranges from 500 to 700 mm in the larger part of the peninsula, reaching 1200 mm in the Khibiny mountains. Winter lasts for some seven months and summer for some three months, with a mean annual temperature of 0 to -1 °C and winter minimum temperatures falling as low as -47 °C.

Experiments **III** and **IV** were conducted with mountain birch seedlings naturally recruited in unpolluted and sheltered conditions some 15 km SE of Kirovsk (67°32'N, 33°57'E). The seedlings in experiment **V** were grown from seeds collected from two stress gradients: an elevation gradient on the southern slope of the Lovchorr (Raswumchorr) mountain in the central Kola Peninsula (67°35'N, 33°45'E), and a

seashore gradient on the shore of the White Sea in the southern Kola Peninsula near the mouth of the river Olenitsa (66°28'N, 35°12'E). In experiment **VI**, in addition to the previous two gradients, seedlings derived from a pollution gradient south of the Severonikel copper-nickel smelter in Monchegorsk in the central Kola Peninsula (67°55'N, 32°48'E) were also used. The seedlings in experiment **V** were derived from one source site per gradient, while in experiment **VI** I used seedlings from the extreme (high- and low-stress) ends of each gradient. In addition, for experiment **I** seeds were collected from the extreme ends of three additional gradients: a pollution gradient south of the Pechenganikel copper-nickel smelter in Nikel in the northwest Kola Peninsula (69°24'N, 30°16'E), an elevation gradient on the southern slope of the Kukisvumschorr (Vudjavr) mountain in the central Kola Peninsula (67°41'N, 33°39'E), and a seashore gradient on the shore of the White Sea in the southern Kola Peninsula near the mouth of the river Lodochnyi (66°17'N, 35°24'E). The seedlings used in experiment **II** originated from multiple sites of varying pollution stress and wind exposure (see Table 1 in **II**).

The high-stress sites of the pollution gradients were located near (1 – 8 km distance) the copper-nickel smelters in so called industrial barrens (Figure 2), with very low (< 5%) vegetation cover and high physical stress (Kryuchkov 1993; Mikkola 1996; Rigina & Kozlov 1999; Kozlov 2001, 2002; Kozlov & Zvereva 2007). Before human impact, the areas now transformed into industrial barrens consisted of mixed forests of mountain birch, Scots pine and Norway spruce around Monchegorsk (Bobrova & Kachurin 1936) and of mountain-birch-dominated forests around Nikel (Valle 1933). Nowadays, after some 70 years of heavy metal and SO_2 emissions (Boyd *et al.* 1997; Gregurek *et al.* 1998; Kozlov & Barcan 2000; Barcan 2002), the areas surrounding the copper-nickel smelters have suffered extensive forest decline, followed by the destruction of ground level vegetation and the uppermost soil layers (Kryuchkov 1993; Kozlov & Zvereva 2007). The industrial barrens are dominated by dead tree trunks, stunted polycormic mountain birches and willows (*Salix caprea* L., *S. myrsinifolia* subsp. *borealis* (Fr.) Hyl.) and occasional patches of dwarf shrubs (*Vaccinium myrtillus* L., *V. vitis-idaea* L., *Empetrum nigrum* subsp. *hermaphroditum* (Hagerup) Böcher) and grasses (mainly *Deschampsia flexuosa* L.). Due to forest decline, the industrial barrens also suffer from excessive wind speeds (Kozlov 2002; Kozlov & Zvereva 2007) and temperature extremes resulting from the lack of shade and the thinning of the insulating snow cover (Hepting 1971; Wołk 1977; Kozlov & Haukioja 1998; Kozlov 2001; Kozlov & Zvereva 2007).

Figure 2. Typical high-stress study sites at the pollution gradient near Monchegorsk (above), the elevation gradient of the Lovchorr mountain (middle), and the seashore gradient near Olenitsa (below).

The high-stress sites in natural gradients were located in open, wind-exposed sites with very little shelter from the topography or surrounding vegetation (Figure 2), for example close to the seashore or above the altitudinal timberline. Like the industrial barrens, the non-polluted high-stress sites were characterised by strong winds (see Table 1 in **VI**; Ruotsalainen *et al.* 2008) and sparsely growing low-stature birches and willows (Figure 2). Unlike the industrial barrens, the field layer vegetation in natural gradients did not vary significantly with stress level (see Table 1 in **VI**). The field layer vegetation in the wind-exposed sites consisted mainly of *E. n.* subsp. *hermaphroditum*, *V. myrtillus*, *V. vitis-idaea*, *Calluna vulgaris* (L.) Hull. and *Betula nana* L.

All source sites classified as control (non-polluted) were located at least 12 km from the nearest smelter in areas of "invisible pollution"; in other words, pollution loads were close to background levels (max. 5% foliar Ni and Cu compared to polluted source sites) and no visible pollution damage was detected in the vegetation (Kozlov 2005b). The low-stress sites of the natural gradients were sheltered from wind (see Table 1 in **VI**) and temperature extremes by abundant surrounding vegetation (Figure 3). All the low-stress sites (in both pollution and natural gradients) were located in healthy boreal forests, dominated by mountain birch, Scots pine and Norway spruce (Figure 3), and with ample field layer vegetation (see Table 1 in **VI**), consisting largely of the same species as in the wind-exposed sites.

Figure 3. Typical low-stress study site.

2.3. Experimental setup

2.3.1. Local adaptation, co-resistance and trade-offs

Experiments **I** (2005) and **II** (2003-2006) were conducted to study potential local adaptations to heavy metals and natural abiotic stress, i.e. wind and drought, by exposing seedlings from the high- and low-stress ends of each study gradient to their native stressors. Seedlings from natural stress gradients were also exposed to heavy metals, as were seedlings from pollution gradients to natural stressors, to determine whether adaptation to one stressor has resulted in increased resistance to other forms of stress (co-resistance / co-tolerance), or whether local adaptation carries a cost in the form of weakened performance under other stressors (trade-off). Since exposure to a stressor can harden plants to better tolerate different future stressors (Atkinson *et al.* 1988; Kozlowski & Pallardy 2002), a response easily mistaken as co-resistance, the plants were grown from seeds to minimise these maternal effects (Roach & Wulff 1987). Experiment **I** was conducted in a common garden in the greenhouse of the Ruissalo Botanical Garden, Turku, and experiment **II** in common gardens (a) in the greenhouse of the University of

Tromsø, Norway, and (b) on wind-exposed and sheltered sites in northern Norway near Kilpisjärvi (69°07'N, 20°45'E) and Narvik (68°31'N, 17°58'E).

2.3.2. Shelter effects and spatial variation in adult-seedling interactions in industrial barrens

Experiments **III** (1999-2004) and **IV** (2000-2005) were conducted in two industrial barren sites near the Severonikel copper-nickel smelter (see Table 1 in **IV**). Both experiments were aimed at observing the effects of shelter in wind-exposed industrial barrens. Experiment **III** was conducted to verify the negative effects of wind-related stress (and the positive effects of shelter) on mountain birch seedlings by using various abiotic wind shelters (see also Eränen & Kozlov 2007), and to quantify the importance of shelter in relation to the amendment of soil toxicity. Experiment **IV** was conducted to determine how biotic shelters modify the surrounding microenvironment and how the interplay between competition and facilitation between conspecific adults and seedlings varies at different planting distances.

2.3.3. Plant-plant interactions in relation to stress

Experiments **V** and **VI** (2004-2007) were conducted at the high- and low-stress ends of the Monchegorsk (**VI**), Lovchorr (**V**; **VI**) and Olenitsa (**V**; **VI**) stress gradients (see 2.2). Both experiments were conducted to study SGH in multiple stress gradients. In addition, in experiment **V** I wanted to see how plant size and ontogenetic stage (adult-seedling and seedling-seedling interactions) affects the balance between competition and facilitation. The effects of seedlings on adult hosts were expected to be minor, and were outside the scope of the thesis. In experiment **VI** I used seedlings from the extreme ends of each study gradient, to find out if environmental conditions at the source sites have resulted in local adaptations and how seedling origin affects their competitive ability and facilitative responses.

2.4. Plant performance variables and statistical analyses

In all the experiments (**I – VI**) I quantified plant growth by measuring leaf length and seedling height, and monitored the survival of the study seedlings. In experiments **II** and **III** I also measured the length of long shoots, in experiment **II** the number of long shoots as well. Long shoots grow tens of millimetres per year, produce several leaves and are responsible of canopy expansion, while short shoots grow a few millimetres per year, producing only two to five leaves. In addition to growth, the number of long shoots can be interpreted to represent growth form, with polycormic, bush-like birches having more long shoots than monocormic, tree-like birches. Plant stress was quantified by measuring chlorophyll fluorescence (**I**; **II**; **III**; **V**; **VI)**, and fluctuating asymmetry (**II**). The proportion of leaves damaged by insect herbivores was measured in experiment **II**. Population differences in phenotypic plasticity were quantified with the relative

distances plasticity index (RDPI, sensu Valladares *et al.* 2006) in experiments **II** and **VI**. The data were analysed with correlation analyses (**I**; **II**; **IV**), ANOVAs (**I** – **IV**; **VI**) and ANCOVAs (**II**; **V**; **VI**), including the use of repeated measures (**I** – **VI**) and nested variables (**I**). Seedling survival was analysed either with logistic regression (**III**) or the Cox regression (**I**; **IV**; **V**; **VI**). Survival in experiment **II** was 100% and was thus not analysed.

3. RESULTS AND DISCUSSION

3.1. Microevolution, or the lack thereof, in contrasting environments

3.1.1. Rapid heavy-metal adaptation around copper-nickel smelters

Articles **I** and **II** provide evidence of rapid parallel evolution towards heavy-metal resistance in mountain birch populations located around the copper-nickel smelters in Monchegorsk and Nikel. While there have been numerous studies documenting heavy-metal adaptations in annuals and short-lived perennials (e.g. Gregory & Bradshaw 1965; Simon 1978; Bradshaw & McNeilly 1981; Coulaud & McNeilly 1992; Macnair 1997; Chardonnens *et al.* 1999; Rengel 2000; Zalecka & Wierzbicka 2002; Przedpelska & Wierzbicka 2007; Dechamps *et al.* 2008), pollution-driven evolution in long-lived trees has been documented very rarely; interestingly, usually in birches or willows (Denny & Wilkins 1987; Eltrop *et al.* 1991; Watmough & Dickinson 1995; Utriainen *et al.* 1997). Population differences in heavy-metal resistance were detected in different performance variables in each experiment, probably reflecting the different amounts of heavy metals applied. In experiment **II**, where the heavy-metal addition was much more moderate than in experiment **I** (as shown by the 0% mortality in experiment **II**), differences in heavy-metal resistance were visible only in chlorophyll fluorescence, not in growth characteristics. In experiment **I**, with ~85% mortality, the superior heavy-metal resistance of seedlings originating from industrial barrens was also seen in growth and survival. Article **II** shows that seedlings from industrial barrens had lower foliar nickel concentrations than seedlings of control origin, indicating that heavy-metal adaptation in mountain birch may be due to reduced heavy-metal uptake. The growth form in populations of polluted origin may also reflect a genetic response to stressful conditions (**II**), but mountain birch phenology has remained unaffected by the impact of pollution (Kozlov *et al.* 2007). While the literature distinguishes between stress tolerance, i.e. reducing the negative effects of damage, and resistance, i.e. reducing the damage itself (Strauss & Agrawal 1999; Agrawal *et al.* 2004), the terms are often used interchangeably. In the case of Kola Peninsula mountain birch, given that reduced nickel uptake is behind the heavy-metal adaptation observed, the adaptive mechanism can be termed resistance in the strict sense. The adaptation, however, may be the result of multiple mechanisms, with increased heavy-metal tolerance (Denny & Wilkins 1987) and adaptation to the better use of mycorrhizal fungi against heavy metals (Brown & Wilkins 1985; Jones & Hutchinson 1986; Jentschke *et al.* 1999) possibly having an effect that could not be detected in these experiments. Also, while it is possible that maternal effects may have contributed to some non-genetic variation between the study populations, their impact was minimised by germinating the study plants from seeds in controlled conditions (Roach & Wulff 1987).

Rapid evolution at contemporary time scales can occur when new environments are colonised or due to strong divergent selection in heterogeneous environments (Orr & Smith 1998; Kinnison & Hendry 2001; Reznick & Ghalambor 2001; Kawecki & Ebert 2004; Barrett & Schluter 2008). In extreme cases selection has been shown to result in evolutionary change in just a few generations (Huey *et al.* 2000; Franks *et al.* 2007; Van Doorslaer *et al.* 2007). Here the heavy-metal adaptation has occurred over approximately 70 years, i.e. one to two generations, suggesting extremely strong evolutionary forces. The very low tree densities near the smelters (Kryuchkov 1993; Kozlov & Zvereva 2007) and the results of earlier studies (Pankratova 1991; Kozlov & Haukioja 1999; Kozlov 2005a; **III**; **IV**) suggest very high mortality and low seed germination, probably resulting in extremely strong directional selection towards heavy-metal resistance in industrial barrens. Given the high genetic variation in *B. pubescens* of northern Europe (Eriksson & Jonsson 1986; Howland *et al.* 1995), the heavy-metal resistance detected in mountain birch, and its appearance in just one or two generations, is most plausibly explained by strong survival selection from standing genetic variation (Hoffman & Parsons 1991; Barrett & Schluter 2008) via total elimination of sensitive genotypes.

3.1.2. Secondary effects of heavy-metal adaptation

Adaptation, however, was not without cost. Heavy-metal-adapted seedlings showed weakened performance in control conditions (**I**) and in drought treatment (**II**). The trade-off observed is consistent with current theory, according to which adapting to a specific stressor is costly and will result in decreased performance under conditions in which the trait is not needed, effectively preventing the adapted genotype from spreading to the whole population (Futuyma & Moreno 1988; Hoffman & Parsons 1991; Kawecki & Ebert 2004; Bijlsma & Loeschcke 2005; Roff & Fairbairn 2007; Barrett & Schluter 2008). Trade-offs in relation to heavy-metal adaptation are often associated with the reduced competitive ability of adapted genotypes (Hickey & McNeilly 1975; Dunson & Travis 1991), but in the case of heavy-metal-adapted mountain birch the effect of competition was similar irrespective of seedling origin (**I**), suggesting that the trade-off is the result of general growth retardation, not decreased competitive ability.

The maladaptation of heavy-metal-adapted seedlings to drought (**II**) was surprising, given that exposed sites, despite higher amounts of rainfall received (due to lack of canopy interception) (Matlack 1993; Callaway 2007), are often associated with water deficit driven by extreme evaporation (McLeod & Murphy 1977; Ko & Reich 1993; Man & Lieffers 1999; Callaway 2007). Drought is a widely assumed stressor in industrial barrens as well (Wołk 1977; Kozlov & Haukioja 1999; Winterhalder 2000; Kozlov *et al.* 2000; Kozlov & Zvereva 2007), and in some cases heavy-metal-resistant plant populations are also characterised by increased drought tolerance (Sgherri *et al.* 2001; Zalecka & Wierzbicka 2002), possibly driven by pleiotropy and/or selective forces operating in the drought-prone barren sites. The observed maladaptation should not be

interpreted as absence of drought stress in industrial barrens, but rather as evidence of extremely strong past selection pressure imposed by heavy-metal pollution.

While co-resistance between different forms of abiotic stress has been documented at the level of physiological acclimation (Atkinson *et al.* 1988; Kozlowski & Pallardy 2002), and genetic adaptation (Watmough & Dickinson 1995; Utriainen *et al.* 1997; Sgherri *et al.* 2001; Zalecka & Wierzbicka 2002), in my data heavy-metal-adapted seedlings did not show increased tolerance to drought or wind stress (**II**), and seedlings from naturally stressful habitats were not co-resistant to heavy metals (**I**; **II**), providing no evidence for co-resistance between different forms of abiotic stress.

In contrast, heavy-metal-adapted seedlings did show co-resistance to biotic stress; they were consumed by insect herbivores to a lesser extent than were control seedlings (**II**). Co-resistance to herbivory in heavy-metal-adapted genotypes has been detected in several taxa (reviewed by Poschenrieder *et al.* 2006), but the increased defence has always been attributed to heavy-metal-derived mechanisms, such as phytosanition or metal fortification (e.g. Mittra *et al.* 2004; Mithofer *et al.* 2004; Nelson & Citovsky 2005). In this case, however, as the seedlings were grown from seeds under conditions of background (i.e. very low) pollution, heavy-metal-derived defences are out of the question. The leaf weight/area ratio was unaffected by seedling origin, suggesting that the co-resistance is not a result of changes in leaf physical structure, but rather in physiological or chemical characteristics. To my knowledge, article **II** provides for the first time evidence of co-resistance to herbivory in heavy-metal-adapted plants irrespective of local heavy-metal concentrations in plant tissues or the surrounding environment.

3.1.3. No adaptive population differences in natural stress gradients

No local adaptations to natural stress (wind, drought) were observed (**II**; **VI**), despite some 10 000 years of evolution at the study sites since the last ice age (Aas & Faarlund 2001). This is rather surprising, given the potential of Kola Peninsula mountain birch for rapid (60 to 70 years) evolutionary change (**I**; **II**). The lack of local adaptations in exposed environments is in contrast with a large number of studies showing home-site advantages in gradients of abiotic stress (Miller & Weis 1999; Byars *et al.* 2007; Savolainen *et al.* 2007; Ohsawa & Ide 2008). Factors possibly favouring generalisation or phenotypic plasticity (as opposed to adaptation) in the natural gradients studied include strong pollen-driven gene flow (Linhart & Grant 1996; Nunney 2001; Kingsolver *et al.* 2002; Savolainen *et al.* 2007), great year-to-year variation in summer growth conditions (Bakkal 1990; Valkama & Kozlov 2001; Futuyma 2001; Kingsolver *et al.* 2002) and small differences in selection pressure when compared to the evolutionary histories in the pollution gradients (Pankratova 1991; Kryuchkov 1993; Kozlov & Haukioja 1999; Kozlov 2005a). Another point to consider is the strong positive effect of nurse trees on mountain birch seedlings growing in exposed habitats, as seen in article **V**. Recently, the role of facilitation in plant evolution has received some due attention,

with niche construction by nurse plants suggested to promote biodiversity by creating favourable conditions for plants that would otherwise become extinct (Valiente-Banuet *et al.* 2006; Lortie 2007). I suggest that in my study system niche construction by nurse plants may have had an opposite effect, with facilitative interactions resulting in lowered biodiversity. Refuges created by adult conspecifics may reduce the need to adapt to wind-induced stress (Odling-Smee *et al.* 1996; Laland *et al.* 1999), promoting generalisation and phenotypic plasticity over diversifying genetic adaptation. In pollution gradients the situation is different, as the adult hosts are unable to create refuges against heavy-metal pollution. On the contrary, they can trap pollutants, creating even less favourable growth conditions (Lukina & Nikonov 1999; Ginocchio *et al.* 2004). This disparity in primary stress factors and the effects of the extant vegetation may explain why mountain birch populations show no adaptations to natural stress (**II**; **VI**), despite their capacity for rapid evolution (**I**; **II**). However, as selection pressure can vary with time and between life-history stages (Geber & Griffen 2003; Metcalf & Pavard 2007), the possibility that local adaptations to natural abiotic stress might be detectable during more stressful years or later life-history stages should not be overlooked.

Although I did not detect local adaptations to natural abiotic stress, there were some differences between populations from contrasting environments. The differences either did not satisfy the criteria suggested by Kawecki and Ebert (2004) as proof of local adaptation (**I**; **II**; **VI**) or were indicative of maladaptations to local conditions (**II**). It is, however, important to note that the supposed maladaptations to local conditions were not observed in reciprocal transplant experiments but in common garden conditions, suggesting that they may be due to differences between experimental and natural environments (**II**). Interestingly, article **VI** gave evidence of a home-site advantage in low-stress populations, but populations from conditions of high abiotic stress did not show increased performance in their corresponding local conditions. This finding is surprising; poor performance in non-local conditions together with no detectable home-site advantage should be maladaptive in a global sense, and disappear in the course of evolution. However, there are some mechanisms that could result in such an unexpected phenomenon. First, high phenotypic plasticity, i.e. the capacity of a single genotype to produce different phenotypes depending on the surrounding environment (Via *et al.* 1995; Schlichting & Pigliucci 1998; Pigliucci 2001; Kingsolver *et al.* 2002; Nussey *et al.* 2007), can be detrimental in conditions of severe directional selection, when any deviation from the optimal phenotype is selected against (Taylor & Aarssen 1988; Emery *et al.* 1994; Heschel *et al.* 2004). Such a phenomenon could result in a population of extremely low phenotypic variation, creating a selective disadvantage in non-local conditions. Indeed, article **VI** gave some indication of lower phenotypic plasticity for mountain birches of high-stress origin in the elevation gradient. The poor performance of elevation-gradient high-stress seedlings in conditions of low stress can thus be tentatively attributed to the elimination of plastic genotypes. Finally, adaptively neutral mechanisms, such as

population bottlenecks and genetic drift, can affect the genetic structure of populations especially in cases of high random mortality (Futuyma 2001; Turelli *et al.* 2001; Kawecki & Ebert 2004). As no differences in plasticity were detected in the seashore gradient, I suggest that underlying the differentiation observed in the seashore gradient are neutral evolutionary mechanisms; the close to 100% mortality of unprotected seedlings (**V**; **VI**) may have inflated the effects of random mutations and bottlenecks, resulting in evolutionarily neutral differentiation despite the balancing effects of gene flow.

3.2. Intraspecific competition and facilitation in contrasting environments

3.2.1. Stronger net facilitation in high-stress environments

The results from host-seedling interactions in article **V**, together with the stronger seedling-seedling competition in low-stress environments (**VI**), provide support for the stress-gradient hypothesis (SGH), according to which facilitation should increase relative to competition with increasing abiotic stress (Bertness & Callaway 1994; Holmgren *et al.* 1997; Brooker & Callaghan 1998; Callaway 2007; Brooker *et al.* 2008). While my experimental design did not allow testing the alternative 'humpback' hypothesis, (Maestre & Cortina 2004; Maestre *et al.* 2005; Gilad *et al.* 2007), the consistent results from two different stress gradients and with various performance variables (both growth- and photosynthesis-related) provide solid support for SGH and its generality in subarctic environments. Although it is possible that a decrease in net facilitation takes place under conditions of extremely high stress (as suggested by the humpback model), the clear support for SGH, together with the verified high stress at the studied high-stress sites (e.g. with 95.6% mortality of non-sheltered seedlings in the seashore-gradient high-stress site) suggest that the possible decrease in facilitation at the extreme high-stress ends of the study gradients is of minor effect. An important point to take into consideration is the nature of the main stressor: in studies that support the humpback model, nutrient deficiency and drought, i.e. 'resource stressors', are considered the most important abiotic forces affecting plant-plant interactions (Rebele 2000; Maestre & Cortina 2004; Maestre *et al.* 2005; Gilad *et al.* 2007), whereas in my study system a 'non-resource stressor', wind (see below), is expected to be of greatest importance. In other words, while extreme shortage of a primary plant resource (such as nutrients or water) might be expected to cause strong competition, possibly shifting the balance away from facilitation at the extreme end of the stress gradient, increasing competition for a non-resource stressor (such as wind) is a theoretical impossibility. While facilitation itself may decrease in exceptionally severe environments (Michalet *et al.* 2006), the nature of the main stressor (resource vs. non-resource) may be important with regard to the effect of stress on plant-plant interactions.

Although the stronger facilitation at high-stress sites was clear, positive host-seedling interactions also dominate at the low-stress ends of the gradients studied (**V**). Recently,

several authors have emphasised the importance of studying environmental gradients in sufficient 'length', i.e. study sites that differ sufficiently in the impact of the main abiotic stressor (Maestre & Cortina 2004; Maestre *et al.* 2005; Lortie & Callaway 2006; Kawai & Tokeshi 2007; Callaway 2007). In agreement with this suggestion, my low-stress sites were located in typical sheltered subarctic forests (Figure 3), and no sites less perturbed by abiotic stress could be found within reasonable distance. The high-stress sites were correspondingly situated in completely exposed, non-sheltered environments (Figure 2). The sites chosen thus represented the extreme ends of the natural wind-exposure gradients. Since both extremes of the natural stress gradients were studied, I conclude that the host-seedling interactions of mountain birch of the age and size range studied may indeed be facilitation-dominated. The apparent dominance of facilitation at the low-stress sites is probably due to better soil quality close to the hosts. Either the hosts were originally recruited in above-average microsites, soil quality has been ameliorated by the hosts (Callaway *et al.* 1991; Puigdefábregas *et al.* 1999; Armas & Pugnaire 2005; López-Pintor *et al.* 2006), and/or the hosts provide nearby seedlings with faster mycorrhizal colonisation and resources via fungal networks (Kranabetter 1999; Horton *et al.* 1999; Kennedy *et al.* 2003; Nara & Hogetsu 2004; Hasselquist *et al.* 2005; Nara 2006).

The results of articles **III** and **IV** as well as other studies (Carlsson & Callaghan 1991; Sonesson & Callaghan 1991; Olofsson 2004; Eränen & Kozlov 2007; Zvereva & Kozlov 2007) emphasise the importance of shelter in open subarctic environments. Also, although there was some weak indication of seedling-seedling facilitation (**VI**), competition dominated between seedlings, probably due to their weak shelter effects. I therefore suggest that the increase observed in host-seedling facilitation at high-stress sites (**V**) is attributable to the adult hosts sheltering the seedlings from harsh environmental conditions (see Table 2 in **IV**; Table 1 in **VI**). Possible mechanisms of facilitation that are likely to be more important in exposed environments include wind shelter (Carlsson & Callaghan 1991; Sonesson & Callaghan 1991; Gerdol *et al.* 2000; Smith *et al.* 2003; **III**; **IV**; Zvereva & Kozlov 2007), protection from temperature extremes by accumulating litter and snow or by shading (Sonesson & Callaghan 1991; Holmgren *et al.* 1997; Wied & Galen 1998; Breshears *et al.* 1998; Davis *et al.* 1999; Eckstein & Donath 2005; **IV**) and increasing soil moisture due to canopy interception, shading and/or hydraulic lift (Holmgren *et al.* 1997; Caldwell *et al.* 1998; Rigg *et al.* 2002; **IV**). While other mechanisms, such as competition (Grime 1979; Tilman 1982; Grace 1991; Craine 2005) and indirect facilitation via mitigation of competition imposed by field layer species (Levine 1999; Pages *et al.* 2003; Kunstler *et al.* 2006) or interactions with mycorrhizal fungi (Kranabetter 1999; Horton *et al.* 1999; Kennedy *et al.* 2003; Nara & Hogetsu 2004; Hasselquist *et al.* 2005; Nara 2006) may change in relative importance with varying abiotic stress, due to the visible positive effect of abiotic shelters (**III**; Eränen & Kozlov 2007) I suggest that the support for SGH found in this study can be explained by a more

or less classic 'nurse plant' effect (Niering *et al.* 1963; Turner *et al.* 1966; Archer *et al.* 1988; Callaway *et al.* 1996; Callaway 2007).

3.2.2. Spatiotemporal and ontogenetic variation in plant-plant interactions

Although the detected changes in host-seedling interactions support SGH in my study system, plant interactions are confounded by a multitude of abiotic and biotic factors (see 1.3.1). My experiments allowed me to probe some of these factors, including spatial variation in plant interactions and temporal variation potentially arising from plant ontogeny.

3.2.2.1. Spatial variation

The results of article **IV** indicate that plant-plant facilitation is strongest at intermediate distances (25 cm), i.e. approximately ¼ times benefactor height. The result is in accordance with one of the few studies on the spatially disjunct effects of competition and facilitation, where Dickie and his colleagues (2005) found that seedling growth is maximised at intermediate distances; this suggests that competition dominates closer to the benefactor, and the positive effects of facilitation (via levels of mycorrhizal infection) decrease with distance. Likewise in my study system, I suggest that the poor performance of seedlings at extremely short planting distances (10 cm) is due to the negative effects of the benefactors, i.e. resource competition, trapping of pollutants (Lukina & Nikonov 1999; Ginocchio *et al.* 2004) and possible allelopathic effects, dominating over facilitative interactions. The decline in seedling performance at longer planting distances (≥ 50 cm) can be explained by weakening facilitative effects and subsequently higher wind impact, temperature extremes and drought (Table 2 in **IV**). The antagonistic effects of competition and facilitation fit well with the observed peak in seedling performance at intermediate distances from adult hosts. This finding, together with studies indicating that plant interactions do not necessarily change linearly with stress (Rebele 2000; Maestre & Cortina 2004; Maestre *et al.* 2005; Gilad *et al.* 2007), suggests that ecological phenomena do not essentially change in an on/off fashion, but that intermediate levels of stress, distance, herbivory etc. need to be considered.

3.2.2.2. Temporal and ontogenetic variation

Articles **IV** and **V** show temporal changes in host-seedling interactions, but the changes were contradictory: article **IV** showed evidence for increasing facilitation, whereas article **V** indicated decreasing net facilitation with time. Although spatiotemporal variation in environmental conditions may have affected the plant-plant interactions studied (Kikvidze *et al.* 2006; Sthultz *et al.* 2007), the two studies differ in some key aspects, which may explain the discrepancy in results. Experiment **IV** was conducted in an exposed industrial barren, which in addition to wind related stressors was characterised by strong heavy-metal and SO_2 pollution, whereas the increasing competition in experiment **V** was detected in a sheltered and unpolluted low-stress site. The pollutants trapped by adult

hosts (Lukina & Nikonov 1999; Ginocchio *et al.* 2004) may be especially harmful for young seedlings, whose roots have not yet penetrated through the exceptionally polluted top soil (Dickinson *et al.* 1984, 1991; Ginocchio *et al.* 2004), possibly explaining the early dominance of interference at short planting distances in article **IV**.

The emergent competition imposed by adult hosts towards the end of the experiment in article **V** is in agreement with other studies showing a switch from facilitation towards competition as the beneficiary grows and develops (Aguiar & Sala 1994; Kunstler *et al.* 2006; Miriti 2006; Sthultz *et al.* 2007). Susceptibility to abiotic stress (Callaway *et al.* 1996; Goldberg *et al.* 2001), as well as the relative importance of different resources (and the related competition) (Weiner 1990; Muller-Landau *et al.* 2006; Coomes & Allen 2007) is known to vary with plant size and life history stage, promoting size- and ontogeny-dependent variation in plant-plant interactions. I therefore suggest that the temporal switch towards competition in host-seedling interactions is the result of two synergic phenomena: 1) as the seedling develops it becomes less vulnerable to abiotic stress, and thus less affected by facilitation, and 2) its resource acquisition capabilities and needs grow, increasing competition imposed by (and inflicted against) the adult host, resulting in a net switch towards competition. Another marked contrast I found in plant-plant interactions is the dominance of competition in seedling-seedling interactions (**V**; **VI**), while host-seedling interactions are generally facilitation-dominated (**V**). Together, these results may indicate that when plants are of very different size and developmental status, shelter and other beneficial effects of adult hosts result in facilitation-dominated interactions, but between plants of similar size, and thus of similar resource needs and acquisition capabilities, competition becomes more important.

3.3. Interplay between evolutionary history and abiotic stress on plant-plant interactions

In article **VI** I tried to synthesise the two key phenomena in my thesis, local adaptation to abiotic stress and changes in plant-plant interactions in contrasting environments. Contrary to the results of the pioneering study by Espeland and Rice (2007), I did not detect weakened facilitative responses, and only marginal evidence for weaker competitive effects, in high-stress populations. The lack of weakened facilitative responses in high-stress populations is not altogether surprising, given that the interplay between population origin and facilitation was studied only in the context of seedling-seedling interactions, not in host-seedling systems, which show much stronger positive interactions (**V**). Although seedling origin did not affect performance as such, the weaker competition imposed by high-stress origin seedlings can be interpreted as tentative evidence for their weaker competitive ability; a result similar to the trade-offs often observed in stress-adapted populations (Linhart & Grant 1996; Corcket *et al.* 2003; Kawecki & Ebert 2004; Roff & Fairbairn 2007). However, as no home-site advantage

was detected in high-stress populations, this result must be interpreted with caution. The fact that this tentative evidence for variation in competitive ability was only observed in low-stress environments provides some support for the hypothesis that negative biotic interactions are stronger in conditions of low abiotic stress (Grime 1973,1979).

There were some constraints to the study that must be discussed before considering the results as evidence against the conclusions of Espeland and Rice (2007). While fortunate for the surrounding environment, the decline in emissions from the Pechenganikel and Severonikel smelters (Berlyand 1991; Milyaev & Yasenskij 2006) has been detrimental for my experiments, especially in article **VI**. The decreasing emissions, together with negligible field layer competition in the industrial barrens (Table 1 in **VI**), have resulted in a dramatic increase in birch performance at the high-stress sites, effectively turning the studied pollution gradients upside down with respect to birch growth and survival (**VI**). Therefore the only study gradient with documented local adaptation had to be discarded as unsuitable for studies on SGH (in agreement with Lortie & Callaway 2006). The lack of local adaptations in the remaining study gradients, as well as the weakness of seedling-seedling facilitation, may explain why I failed to find support for the study by Espeland and Rice (2007).

3.4. Practical and theoretical implications

3.4.1. Reforestation and responses to human disturbance

According to a traditional view, short-lived species are able to evolve and produce adaptations to contemporary anthropogenic change, whereas long-lived species (such as trees) are much less likely to do so due to their long generation times (Dickinson *et al.* 1991; Turner *et al.* 1991; Turner 1994; Myers & Knoll 2001). While probably true in a theoretical sense, my results to a certain degree challenge this view, with a long-lived tree evolving detectable heavy-metal adaptation within the course of a single human lifespan (**I**; **II**). In recent years the effects of contemporary evolution have also been endorsed by conservation biologists (Stockwell *et al.* 2003; Hufford & Mazer 2003; Kinnison *et al.* 2007). In the case of Kola Peninsula mountain birch, the evidence for rapid evolutionary adaptation may have practical applications in future restoration efforts in industrial barrens, as the use of local seedlings could improve growth and survival, thus increasing the chances of successful reforestation.

Like local adaptation, the plant-plant facilitation observed also has implications for potential restoration efforts. The positive effects are especially interesting in light of the amelioration of growth conditions observed in the industrial barrens (**VI**). With the decreasing effect of heavy-metal pollution (Berlyand 1991; Milyaev & Yasenskij 2006) and non-existent field layer competition (Kryuchkov 1993; Kozlov & Zvereva 2007; **VI**), shelter effects and plant-plant facilitation are likely to increase in importance in the industrial barrens. Despite the strong positive effect of soil amelioration by liming (**III**),

sheltering by abiotic methods (**III**; Eränen & Kozlov 2007) and biotic ones (**IV**) needs to be taken into account in estimating potential natural and artificial re-colonisation. The natural re-emergence of vegetation, and how it is affected by extant adults, is especially important considering that the seed banks of various plant species can retain their viability even under heavy pollution loads in industrial barrens (Komulainen *et al.* 1994), and that mountain birch seed production has remained unhindered by past pollution (Kozlov & Zvereva 2004). Together with studies of other areas degraded by human activities (Castro *et al.* 2002; Gómez-Aparicio *et al.* 2004; Padilla & Pugnaire 2006), my results encourage the use of artificial and natural shelters in efforts to reforest landscapes destroyed by human impact, without necessarily relying on expensive soil amelioration techniques (Cairns 1995; Winterhalder 2000).

3.4.2. Global change

Human activities influence many critical environmental characteristics, including carbon dioxide levels, water and nutrient availability, temperature etc. The rapid evolution observed in a long-living tree species encourages rethinking the effects of local and global anthropogenic change in populations of habitat-forming trees. More specifically for mountain birch, the rapid evolution of heavy-metal resistance (**I**; **II**) together with the lack of adaptation to natural stressors (**II**; **VI**) has interesting implications. It may be that the great but regular annual variation in summer conditions in the Kola Peninsula (Bakkal 1990; Valkama & Kozlov 2001) promotes genetic variation in mountain birch populations (as shown by Eriksson & Jonsson 1986; Howland *et al.* 1995). High levels of specialisation could result in an evolutionary 'dead end' which would be maladaptive in varying environmental conditions. The logic is interesting in the light of the anticipated climate change, as the differences in June temperatures (warmest June 5.1 °C warmer than the June mean sensu Bakkal 1990) are in line with the projected anthropogenic temperature increase of 4 – 7 °C in the northernmost parts of the northern hemisphere over the next 100 years (ACIA 2004).

Summing up: mountain birch may have a good chance of persisting even under human-induced climate change, due 1) to the absence of local adaptations to harsh environmental conditions (and related 'dead ends'), 2) to its great capacity to respond positively to rising temperatures (Ovaska *et al.* 2005), 3) to its potential for rapid evolution (**I**; **II**), and 4) to the fact that potential invasive southern species are not adapted to the 24h summertime light conditions (Wielgolaski & Karlsen 2007).

4. CONCLUDING REMARKS

The central idea behind this thesis was to study biotic interactions and evolutionary responses in gradients of abiotic stress. I hope I have succeeded in convincing the reader that it is essential to take into account both abiotic and biotic factors in order to understand plant performance and the structuring of plant populations. I also hope to have shown with reasonable certainty that mountain birch is capable of rapid evolutionary adaptations, and that intraspecific facilitation is especially important in conditions of high abiotic stress, in accordance with SGH. However, as so often in ecology, the results urge caution in making generalisations, with the lack of local adaptations in natural stress gradients in spite of great differences in survival, and the strong effects of plant ontogeny and planting distance in facilitation strength. The confounding factors, together with the recent advent of the humpback model, suggest that SGH is an overgeneralization, calling for more precise and condition-specific hypotheses. It is to be hoped that future studies, taking into account for example plant ontogeny, differences in stress resistance, and the nature of the main stressor (resource vs. non-resource), will yield information as to when, where, and under what conditions SGH is most applicable, and when more specific models are needed.

In many ways, I have found my thesis work to be representative of the field of ecology in general: the excitement of finding support for a theory turning to frustration when confounding factors ruin all one's beautiful overgeneralisations, followed by the excitement of formulating new ideas to explain the phenomena observed. Here, in the excitement, the frustration, and the unending flood of novel ideas, lies for me the very core of ecology, and why, in all its grandeur and folly, it is such an exciting field of science.

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